Nutrient Dynamics During Terrestial Ecosystem Development: Hypotheses

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Generalization of nutrient conservation with respect to succession is complicated due to specific mineralization rates of organic elements, species nutrient requirements, dependency of element cyclings on soil chemistry and indirect feedback controls of ecosystems as well as net ecosystem production. Elemental specificity on such biogeochemical processes and the influences of successional status and disturbance should be considered in assessing nutrient dynamics during ecosystem development. Here more comprehensive hypotheses are presented to describe nutrient dynamics with terrestrial ecosystem processes. The hypotheses suggest that accumulation rates of nitrogen are highest during the intermediate stages of ecosystem succession. Phosphorus, however, becomes less leacky during ecosystem development due to relatively later and consistent organic accumulation, especially at its limiting soils, a lack of its release from decomposing organic matter in excess of biotic demands, enhanced retention capacity of soil component through soil aggregation, chemical reactivity by organic acids, and biotic consumption including microbial immobilization. Sulfur retention may depend on

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whether its availability is in excess or deficient and if the major supply is from atmosphere or soil components.

I. Introduction

A general principle of succession is that nutrient cycles become closed as ecosystems develop (Odum 1969). Closed nutrient cycles suggest that the dependence of biotic components on internal (within-ecosystem) supply of nutrients increases with ecosystem development, and it is also related to enhanced nutrient conservation capacity in ecosystems. Vitousek and Reiners (1975), in contrast or as an alternative to Odum, proposed the biomass increment hypothesis (BIH), which emphasizes that nutrient retention in an ecosystem is largely dependent on biological tie-up. The BIH suggests that essential nutrient elements are strongly retained during the intermediate stages of ecosystem succession when net ecosystem production is maximal, and nutrient inputs and outputs are eventually balanced at steady state.

Odum (1969) did not mention the specificity of each element in biogeochemical processes, but implicitly considered biologically essential elements. Vitousek (1977) discussed elemental specificity, but placed considerable emphasis on direct incorporation of elements into biomass as nutrient retention mechanism. This may be due to a focus on nitrogen, a frequently limiting essential element in temperate forests. The soil component has often not been included in nutrient bookkeepings of ecosystems except as weathering inputs (Gorham et al. 1979): this is probably due to the usual orientation on presumably homogeneous watershed studies in 1970s. Unfortunately, the outcomes of these types of studies are not applicable to partially disturbed forests and fragmented watersheds. For example, when a riparian ecosystem obtains inflow from nutrient source areas, such as agricultural land and adjacent aquatic systems, the phosphorus budget cannot be explained only by weathering and solubilization of phosphate compounds (Vitousek 1977, Gorham et al. 1979). Such systems become understandable when a different view is taken: soil is a part of ecosystem and of no less importance to ecosystem development than biological components, but rather the two components produce intimately interactive influences on nutrient cycling processes (Webster 1979, Rich

1984, O' Neill et al. 1986, also see Figure 1).

As a matter of fact, there are several weaknesses in the BIH. First, elemental specificity of internal nutrient supply from decomposing organic residues was not considered in the BIH initially (Vitousek and Reiners 1975, Vitousek 1977). Nutrient loss in forest ecosystems is closely associated with its release from decomposing organic residues and incorporation by biotic components as ecosystems

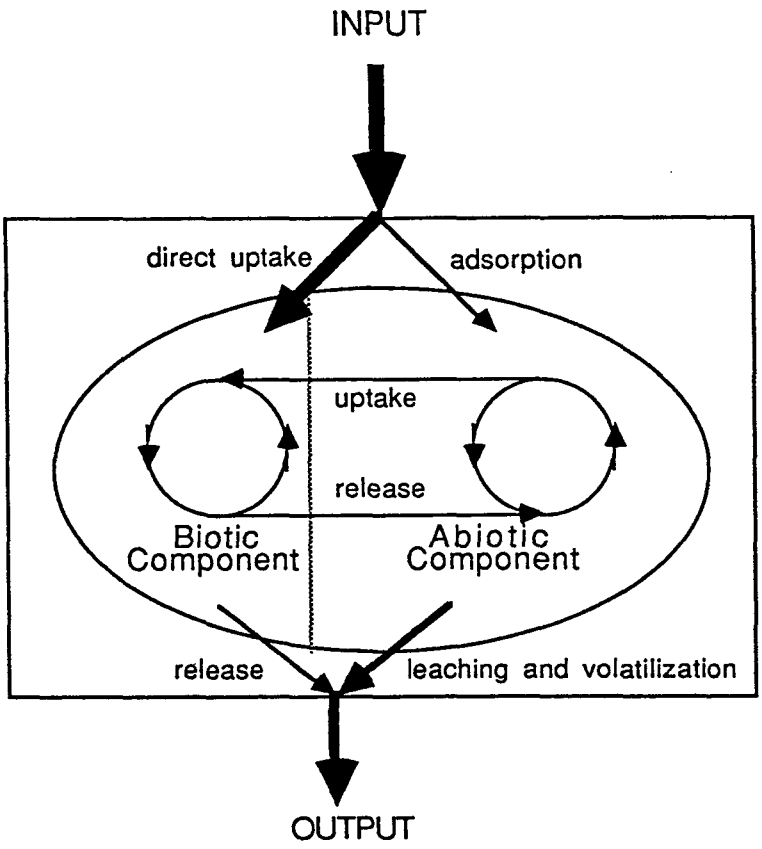

Fig. 1. Schematic diagram showing the importance of both biotic and abiotic components and internal cycle in ecosystems to nutrient conservation. Biotic and abiotic self-cycles are interconnectedly driven by belt of uptake and release (here 'release' includes all processes through which an element leaves from biological components, e.g., excretion, decay and so on). Ellipse indicates that biotic and abiotic components are complimentary part of the other one in ecosystem processes. The areas of dissected ellipse and width of arrow show relative contributions of components and processes, respectively. The relative contributions are variable with element and successional or evolutionary stage. The bigger outside box indicates the capacity enhanced in ecosystem level owing to the interactions of biotic and abiotic processes.

become mature (Sprugel 1984). Considerable information on decomposition dynamics has accumulated during the last decade. For instance, McGill and Cole's (1981) work enables comparison of mineralization of organic carbon (C), nitrogen (N), sulfur (S) and phosphorus (P) in a dichotomous system: biological and biochemical mineralization. This elemental specificity of mineralization of organic elements has been included in the recent papers (e.g., Vitousek and Walker 1987), but is reviewed for further insights in the present study. Second, biological incorporation of all nutritional elements is not synchronous during ecosystem development since the ratio of elements required by biotic components is species-dependent, and there are floristic and other organismic relays representing succession. Consideration of this asynchronism can improve the idea of BIH further. Third, the BIH overemphasizes biological conservation since attention was focused on N. Some nutrient elements are more dependent on chemical than biological processes for conservation, which results in a different relationship between nutrient conservation and ecosystem development. Nutrient elements in biomass do not all originate from easily leachable or volatile forms: some fractions of P may be transformed from relatively conservative to bioavailable forms in soil minerals and taken up by microorganisms or plant roots, and thus not be leachable even without biological uptake. Fourth, the hypothesis does not consider indirect feedback processes. The importance of indirect and positive feedback controls has been recognized in studies of natural systems (Anderson et al. 1985, Vanermeer et al. 1985, DeAngelis et al. 1986, Wilson 1986). The present study introduces some examples of controls by which later successional ecosystems positively enhance nutrient retention.

II. Objectives and Approach

Major objectives of this study are to clarify the Odum vs. Vitousek-Reiners controversy by analyzing appropriate information and to provide a comprehensive model to describe nutrient dynamics during ecosystem development. The controversy between Odum (1969) and Vitousek and Reiners (1975) may be semantic depending on the definition of 'conservation' or 'retention'. The former viewed retention as total amounts of nutrient elements stored in ecosystems, while

the latter tried to define it as a response of ecosystem to external nutrient supplies (Henderson and Westman 1975). This study accepts the latter's option because it can provide additional insights (Vitousek and Reiners 1975). Nutrient loss from a system is then estimated by differences between external and internal supply and internal demand (Gorham et al. 1979). Theoretically, nutrient loss is expressed by a simple mass balance: Loss = Supply - Demand. Nutrient retention is inversely related to its loss and is defined by INPUT - OUTPUT or INPUT/OUTPUT.

To validate the existing nutrient retention models, we need to include all major nutrient sources and sinks and to determine if there are quantitative differences in release from sources and incorporation into sinks along successional stages. Here I review major component processes influencing nutrient budgets in terrestrial ecosystems. Attention is directed to elemental specificity of biological incorporation, abiotic retention, and mineralization of organic materials, and relevant feedback controls because they are major controlling factors of nutrient budgets. The review is restricted to vegetational, microbial and geochemical processes on C, N, S, and P. Although animals influence the mineralization of organic matter, nutrient dynamics and plant community composition in ecosystems (Anderson et al. 1985, Gibson et al. 1987), these factors will not be discussed here. On the basis of this review, some improvements are suggested for the BIH. It is noted that through this paper succession represents primary succession unless specified.

III. Biotic Sinks

The existing models describing nutrient retention in developing ecosystems emphasize the large amounts of nutrients tied up in biomass. Plant biomass is a major biotic nutrient sink due to its relatively large fraction of total biomass. However, microbial biomass is also an important sink, especially during the aggrading phase of disturbed ecosystems due to rapid uptake of dissolved nutrients (Cole et al. 1977, Vitousek and Matson 1984, 1985). Although the data are meager, zoobiomass may also be a significant sink, especially in case of P due to relatively high concentration of the element in faunal components (see Table 1).

Table 1. Atomic ratios of carbon, hydrogen, oxygen, nitrogen, and sulfur to phosphorus in natural compartments (data combined from Bolin et al. 1983 and Reiners 1986)

Compartments	C	H	O	N	S
Fossil fuel emission	9300	—	—	36	130
Combustion of biomass	920	—	—	20	1
Soil organic matter	54	—	—	3	1.2
Terrestrial bacteria	43	76	15	4.3	0.2
Terrestrial fungi	188	342	132	11.7	0.8
Herbaceous angiosperms	230	337	157	23	<1
Woody angiosperms	1103	1618	754	53	5
Insect	68	133	37	16	<1
Mammals	29	48	8	4	<1
Marine phytoplankton	53	130	77	11	<0.1
Marine zooplankton	143	207	74	26	—
Marine crustaceans	115	207	86	21	<1
Marine mollusks	789	2278	19	136	5
Marine fish	68	117	31	14	<1

Later successional plant species are large, relatively slow growing, long-lived and nutrient-conservative and tend to synthesize recalcitrant materials using relatively more C per nutrient minerals (Skujin and Klubek 1982, Grime and Hodgson 1987). Refractory carbohydrates probably result from the need for structural tissues to compete and use light efficiently and as defense against herbivores. The three-dimensional structure of vascular plants has an advantage over two dimensional algae by increasing photosynthetic surface area but it also requires supporting tissues. The defensive function is illustrated by the fact that late successional plants are characterized by lower palatability to generalized herbivores than early successional species (Cates and Orians 1975). It is clear that later successional plants produce recalcitrant materials supplying lower nutrient elements for microbial metabolism than organic C as an energy source. Consequently high ratios of C to nutrients in both organic residues and soils characterize later successional stages.

At the ecosystem level, high ratios of C to nutrients would provide a positive feedback loop to conserve nutrients in the system. Organic matter with high ratios of C to nutrient minerals leads to microbial immobilization of nutrient from the atmosphere and/or soil (Covington 1981, Abbott and Crossley 1982, Skujin and

Klubek 1982, Stevenson 1986). As a result, during later stages of succession, microorganisms immobilize mineral nutrients from the inorganic matrix and thereby contribute to nutrient retention. Hence immediate microbial immobilization of easily leachable inorganic N, P, and other essential elements in the soil solution during later successional stages are reasoned. Since the significance of the microbial pools of nutrients has been recognized, the concentrations of elements in biomass, in addition to all the major biotic nutrient storages, need be considered in the bookkeeping of nutrient elements.

Emphasis on biotic sinks in nutrient conservation led Vitousek and Reiners (1975) to a classification of plant nutrients as nonessential and essential, and limiting and nonlimiting. Essential and limiting elements should be incorporated into biomass very immediately. However, Vitousek and Reiners (1975) failed to consider that elemental requirements differ between biotic groups (see Reiners 1986 for detail). For example, N/P ratios are higher in fungi than in bacteria (Table 1), and bacteria and fungi demonstrate higher ratios of N to C than higher plants (Griffins 1972). Although both bacteria and fungi can incorporate inorganic S into amino acids, only some fungi, not bacteria, are capable of retaining an excess supply of S as HI-reducible organic S compounds in soil systems (Hunt et al. 1983, Stewart 1987). Even species of vascular plants have different requirements for nutrient elements (Bradshaw and Chadwick 1980, Chapin 1980, Tilman 1982). From an individual organism-oriented view on succession (e.g., Huston and Smith 1987), nutritional requirements would vary with the developing stages of a plant species. If there is succession of biotic groups, limiting elements should vary in consequence of biotic requirements and by-products. This is obvious on an evolutionary time scale from the ratios of nutritional elements in biomass as shown in Table 1. The idea seems to be tenable for a successional time scale and is consistent with the idea that biotic groups lead to variation of the available resource-ratio in ecosystems (Rich 1984, Reiners 1986, Miles 1987), which in turn facilitates colonization of other biotic groups or generates new limiting elements (Connell and Slatyer 1977, Tilman 1985).

There may be elemental specificity to losses from ecosystems if the ratios of elements in available forms are not matched with those of the biological requirements. Nutrient release from sources may, to some extent, depends upon

the biotic requirements of the ecosystem. At the same time, initial chemical composition of the substrate governs the release of nutrients from decomposing organic residues (MacLean and Wein 1978, Pastor et al. 1987). Thus, the biotic requirement ratio of nutrient elements is not necessarily correlated with the release ratio from the source. Excess supply beyond biotic demand is destined to be immobilized by abiotic soil constituents or leached out of the system. Abiotic immobilization could then be significant in nutrient retention since only the leached fraction represents nutrient loss from the system.

IV. Abiotic Sinks

There are at least three reasons why abiotic components can be a buffer even during late successional stages when supply exceeds biological requirements. First, nutrient elements originating from soil minerals become depleted during ecosystem development by biological uptake. Hence storage rooms of soil minerals for the elements are relatively enlarged in mature forests. Second, as by-products of organic matter decomposition promote macroaggregate formation in soil (Griffiths 1965, Oades 1984), soil components are able to retain relatively large quantities of nutrient elements (see Elliott 1986). Third, the flux of organic acids during organic matter decomposition makes Al and Fe compounds reactive in adsorbing dissolved anions (Kwong and Huang 1978) and thus reserve a relatively large amount of P in soils (Borie and Zunino 1983, Mamo and Haque 1987). Supply of organic C enhances a very nonleachable fraction of P in soil which is extracted by 0.1 N NaOH solution following sonication (Lee et al. 1990). Richards and Charley (1983) showed that increasing retention of added radioactive P by Australian sandy soil column was accounted for by organic matter. Such geochemical processes and microbial immobilization enhanced by organic C supply are examples of positive feedback controls by which an ecosystem increases both conservation and availability of P and probably other elements, and further accumulation of organic matter in ecosystems (Figure 2 and see Lee et al. 1992 for detail).

In general, retention strength of oxidized forms in soil follows the order: phosphate > sulfate > nitrate (Harward and Reisenauer 1966). Nitrate mobility is largely regulated by biological processes, while phosphate retention depends on soil

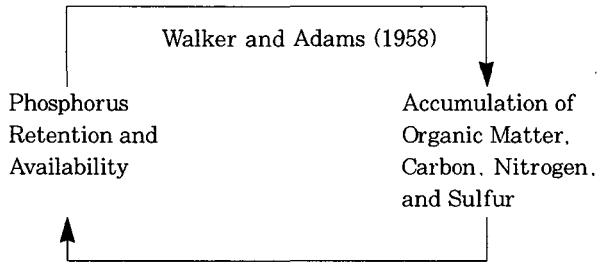

Fig. 2. Interactions of phosphorus and organic matter in soil.

adsorption in forest ecosystems (Johnson and Cole 1980, Wood et al. 1984, Johnson et al. 1986). Nitrate adsorption decreased proportionally to increases in sulfate or phosphate in anion-exchange equilibrium studies (Kinjo and Pratt 1971). A decrease in the adsorption of 1 mole of NO^{3-} corresponded to increasing adsorption of 1 mole of SO_4^{-2} or about 3 to 4 moles of H_2PO^{4-}. Thus, the hypothesis of Vitousek and Reiners would be modified to describe comprehensive element retention in successional forests. Their discussion and data are applied to only those elements which are less adsorptive onto soil minerals (Vitousek 1977).

Sulfate is between nitrate and phosphate in terms of organic matter decomposition and adsorptivity of oxidized elements onto soil minerals. Interestingly, atmospheric supply in natural ecosystems is in the order of N, S, and P. Similar ranking order for biological accumulation of the elements during succession may be found because nutrient availability is largely dependent on atmospheric input and release from soil and decomposing organic matter.

Discussion of the hydrologic regime is indispensable in a review of nutrient dynamics, since water is a major vehicle that transports nutrient elements within and between ecosystems. In the following section, forest hydrology is briefly mentioned. For a detailed review, see Waring and Schlesinger (1985) and Lee et al. (1992).

In describing the nutrient retentiveness of a forest, Knight et al. (1985) have emphasized the hydrologic processes of rainfall interception, evapotranspiration, and hydrograph shape. Hewlett et al. (1984) suggest that the mobility of

nutrients appears to be restricted by the ability of ecosystems to evaporate water on site, which in turn, is associated with vegetative cover. Soil water storage capacity is associated with leaf area index (LAI), due probably to the correlation of LAI and soil organic matter content (Fahey and Knight 1986). Vegetation decreases runoff and, in turn, erosion and nutrient losses, by enhancing evapotranspiration, infiltration and water storage capacity of a landscape. Finally, Knight et al. (1985) conclude that the leaf area of vegetation, duration of the vernal transpiration and high carbon/nutrient ratios in the terrestrial forest floor have critical impacts on nutrient conservation in terrestrial ecosystems. Overland flow is reduced during the later stages of succession due to increasing rainfall interception, transpiration and water-holding capacity of living foliage and forest floors. This suggests that absolute losses of nutrient elements appear to be reduced as ecosystems develop. This is obvious in case of P because most fluvial P exports are in particulate forms and thus positively related to surface runoff discharge (Meyer et al. 1979, Lee et al. 1992).

V. Mineralization of Organic Elements

Release from decomposing organic matter is specific to each nutrient element (McGill and Christie 1983). In general, litter decomposition is initiated by soil cellulase which converts native cellulose to soluble C (Burns 1982). As microorganisms mineralize C, N and C-bonded S in excess of microbial demand are released into inorganic forms simultaneously (called biological mineralization). This concurrent relationship is due to direct linkage of C and N in organic matter (McGill and Cole 1981). This explains why C and N mineralization is closely linked in many cases (McGill et al. 1975), and why organic N and S are mineralized in about the same ratio as they occur in soil organic matter (Tabatabai 1984, Stewart 1987). In many cases, S is closely associated with N in biological systems because both elements are required in protein syntheses.

In contrast, organic P and ester sulfates (HI-reducible S) are linked to C through an ester linkage and mineralized by extracellular enzymes (called biochemical mineralization) independently of organic C and N. Accordingly, S mineralization may not be universally correlated with that of N, and probably

varies with increasing fraction of ester sulfates, much of which is stored in fungi in excess (Hunt et al. 1983). In some cases, organic S undergoes much greater seasonal variation and is depleted faster than organic N (Tabatabai 1984) due probably to large percentage of ester sulfates. McGill and Cole (1981) hypothesize that organic N and C-bonded S are released when microorganisms require C as an energy source, while organic P and HI-reducible S are mineralized as a result of the biological requirement for the elements themselves. This hypothesis implies that release of P from organic matter in excess of biological demands rarely occurs (Vitousek and Walker 1987). Considering that biological uptake, soil adsorption kinetics and transport in runoff are dependent on amounts of bioavailable or labile forms of elements in surface soil (Sharpley et al. 1981), mineralization is a major factor controlling the nutrient retention of an ecosystem. As the source of biologically required nutrient shifts from rock weathering to organic material, the conservation of P and, to some extent, S seems not to follow the hypothesis proposed by Vitousek and Reiners (1975).

VI. Expanded Hypotheses

PRIMARY SUCCESSION. The hypothetical sequence of organic accumulation of nutrient elements in ecosystem during primary succession is presented in Figure 3. In the figure the lines are not necessarily sigmoid. Crocker and Major (1955) demonstrated that total N accumulation in soils of Glacier Bay, Alaska, showed a sigmoid pattern with succession. However, this study highlights asynchronisms of organic accumulation of nutrient elements in ecosystems rather than their graphical forms. It is noted in Figure 3 that the lower curves represent differential functions of upper corresponding ones. By definition, each element is most conservative when it is incorporated in organic forms at maximum rate. Sulfur will be then more conservative in Phase II than in Phase I, in contrast to N. Presumably Vitousek's (1977) data present such cases (Table 2). In a similar way, P retention must become conservative until succession reaches the early Phase III. It is presumed that in many cases natural disturbance may not allow real ecosystems to reach the later Phase III. As a matter of fact, accumulation of soil organic P, even C, N, and S, did not reach an apparent steady state during the

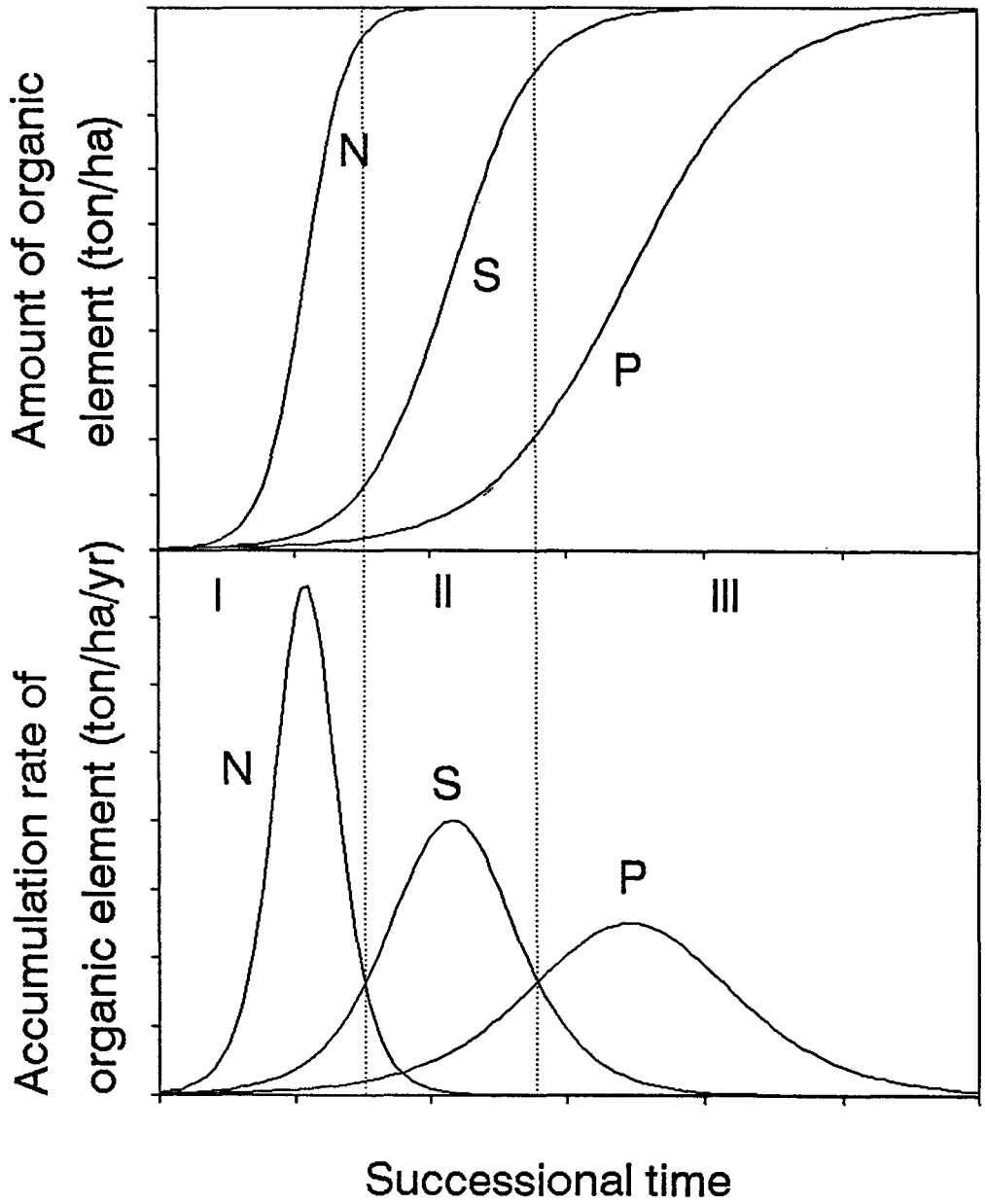

Fig. 3. Hypothetical sequence of accumulation amounts (above) and rates (below) of organic elements during terrestrial ecosystem development. The time scale is not precise and may be varied with ecosystems.

NewZealand Manawatu sand chronosequence even after 10,000 years (Syers et al. 1970, Walker and Syers 1976).

Figure 3 demonstrates that the ratio of N to P in organic matter may increase

Table 2. Mean growing season streamwater concentrations (μeq/litre) from five intermediate-aged successional vs. nine old-aged spruce-fir forest ecosystems, in the White Mountains of New Hampshire, USA (from Vitousek 1977)

Radicals or element	Old-aged	Successional	Ratio of concentrations
NO_3^-	53 (5)[a]	8 (1.3)*	6.62
K^+	13 (1)	7 (0.5)*	1.81
Mg^{++}	40 (4.9)	24 (1.6)*	1.66
Ca^{++}	56 (4.5)	36 (2.5)*	1.55
Cl^-	15 (0.3)	13 (0.3)*	1.16
Na^+	29 (2.6)	28 (0.9)	1.03
SO_4^{2-}	119 (4.6)	123 (6.5)	0.97
Si	75 (7)	86 (5)	0.87
pH	4.92	4.64	

[a]Standard error in parentheses.
*Difference significant at $p<0.05$ level.

with succession initially and then decrease. Nutrient accumulation in biomass must be similar to biological productivity (Vitousek and Reiners 1975). Total nutrient element accumulation is standing crop times the element concentrations in biomass. Standing crop can be calculated by the integration of net production (see Odum 1969, Vitousek and Reiners 1975). The ratio of N to P in biomass may not be constant during succession, because of potentially sequential variations of their use efficiencies and organic accumulation. Meyer et al. (1979) provide the evidence showing that the N/P ratio in fluvial exports is relatively low during the growing season. For instance, the N/P ratios were 16:1 during the growing season and 130:1 during the rest of the year in Bear Brook, New Hampshire. This suggests that biological N uptake is dominant during the growing season, but P uptake, unlike that of N, is not synchronous with biomass increment.

During succession, net gains of N occur because N inputs exceed N outputs. On the other hand, only net loss is expected for P because its atmospheric supply is negligible (Gosz et al. 1973). Phosphorus is exported from terrestrial systems over ecosystem development (Walker and Syers 1976, Schoenau and Bettany 1987). Nevertheless, P loss is reduced with ecosystem development due to lower internal supply of weathering and more P incorporation into organic matter and soil minerals. Sulfur seems to be intermediate because (1) it is mineralized both

biologically and biochemically (McGill and Cole 1981), (2) it is supplied from the atmosphere and soil minerals, and (3) its abiotic adsorption capacity of dissolved forms is between N and P. The relative contribution of biotic and abiotic components to S conservation appears to depend on its supply in an ecosystem. Mineralization of organic S is controlled by its availability in soil, and excess supply is conserved as ester sulfate forms (Hunt et al. 1983, Stewart 1987).

DISTURBANCE. A hypothetical sequence is suggested to describe retention of organic elements in ecosystems against the severity of disturbance (Figure 4). Retention of organic fractions may be determined by sensitivity of elements to microbial mineralization and mobility. Even though microorganisms may prefer compounds containing C, N, S, and P (e.g., phosphate-binding protein; see Anba et al. 1987), carbon compounds are used as their primary energy source. Thus organic C is the first element to be mineralized. Nitrogen is the next because it is directly linked to C through a covalent bond. Detailed explanations for S and P were given previously and are cited in McGill and Cole (1981). The hypothesis suggests that element losses may depend on the severity of disturbance.

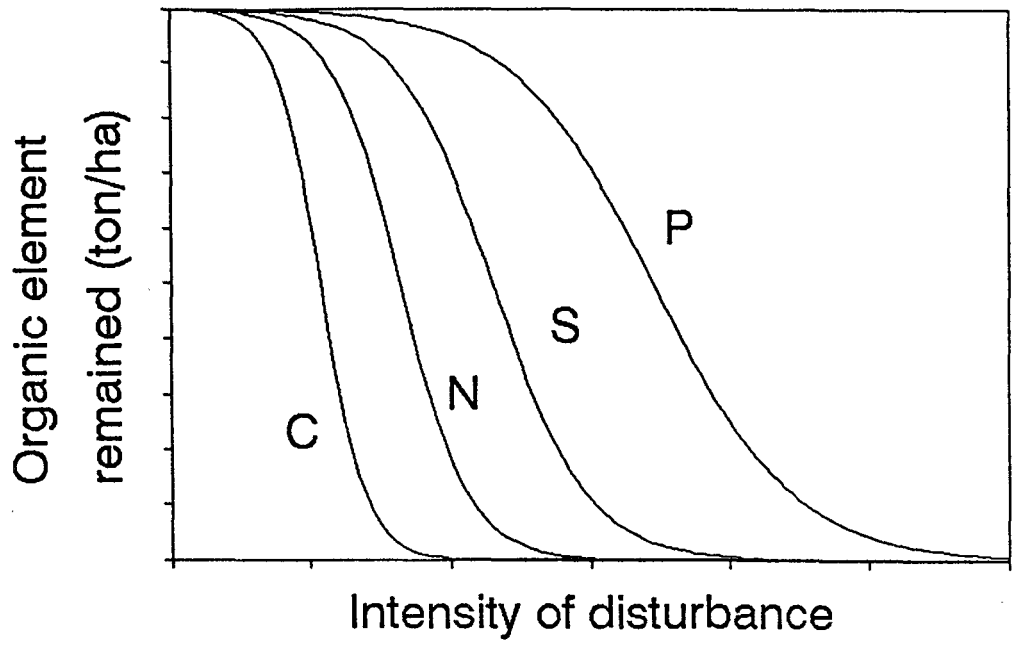

Fig. 4. Hypothetical graph showing relative amounts of organic elements remained in ecosystem against the severity of disturbance.

Consequently, we should consider the severity and history of prior ecosystem disturbance when nutrient element conservation is studied during ecosystem development. Unlike organic C, N, and S, a relatively minor disturbance rarely leads to an extreme loss of organic P in terrestrial ecosystems. This may, to some degree, explain why C/organic P ratios are much more variable than C/N ratio (Stevenson 1986, p.260). Minor disturbances can cause N but not P to become limiting for biomass production.

Until now severity of disturbance has been rarely measured (Van Andel et al. 1987). If the hypothesis of Figure 4 is verified, it may facilitate a quantitative definition for severity of ecosystem disturbance by comparing the amounts and ratios of nutrient elements in ecosystem components immediately after disturbance with reference conditions. It seems that ecosystem resilience may be, to some extent, predictable by the nutrient ratios.

SECONDARY SUCCESSION. In the present section, I compare dynamics of a mobile element, N, and a much less mobile element, P, during secondary succession of a terrestrial ecosystem. It is initially assumed that N and P follow similar patterns in release from decomposing organic residues and in biotic accumulation. In reality, mineralization of organic P is independent of that of N (McGill and Cole 1981), but release patterns are not much different when the ratios of biotic requirements are not significantly different (for example, see Swift and Boddy 1982, Seastedt 1988). Immediately after disturbance, lively microbial activity is expected due to the increased soil temperature and energy source availability. Thus higher fluxes of N and P occur in response to decomposers' energy and nutrient needs. Then the total amount of nutrients released from the organic matter is reduced due to initial high consumption and a lack of litterfall. As ecosystems develop, the nutrient supply rises with increasing organic matter until a steady state is reached.

The ratio of N to P in the biomass may be variable during secondary succession for the same reasons as in primary succession. Organic N is quickly lost after disturbance (Figure 4) and is accumulated during the aggrading phase of ecosystems (Figure 3 and 5), compared to organic P. It appears that P flux from decomposing materials is buffered by absorption of organic residues, microorganisms and algae, and diluted by later successional plants. Microbial

conservation was reported for N (Vitousek and Matson 1985). Relatively high microbial conservation of P may also occur due to biochemical mineralization and a lack of atmospheric loss. This hypothesis is supported by the relatively low values of N/P ratios in organic matter and microorganisms (Table 1).

A net loss of N from an ecosystem is expected during the early stages of secondary succession due to very low adsorption of mobile N forms on soil particles. Budgets of S and P may depend on the severity of disturbance. From the intermediate stages of secondary succession, nutrient retention appears to follow a pattern similar to primary succession. Severity and history of the disturbance are, however, major factors influencing the dynamics of nutrient elements in secondary succession.

VII. Further Verification.

The sequence proposed with respect to accumulaiton of organic elements during ecosystem development is consistent with a computer-simulated outcome of organic element accumulations in grassland soils (Parton et al. 1988). As herbaceous plants are replaced by woody angiosperms during successional seres, organic N will be accumulated more than P (Table 1). On the other hand, amount of organic P will be relatively increased during later succesional seres, as stored in organic matter and microorganisms, and mammals whose N/P ratios are low.

Concentrations of elements present in plant tissues or as plant-available forms in soil may be a better indirect indicator of their potential losses from ecosystems. Sprugel and Bormann (1981) presented data showing that soil nitrate and leaf tissue N were at high levels just after ecosystem disturbance, declined in the following stage, and then increased slightly in old stands. This may corroborate the concept that N loss follows the BIH if nutrient desorption by surface and subsurface waters is proportional to the amount of labile or bioavailable chemical forms present in soils. Boring et al. (1988) also presented data showing slower accumulation rate of P than N in aboveground biomass at Coweeta, North Carolina over three years following clearcutting (Figure 5). Montes and Christensen (1979) demonstrated that dilute acid extractable P in soils decreased with successional age even though its difference was not statistically significant.

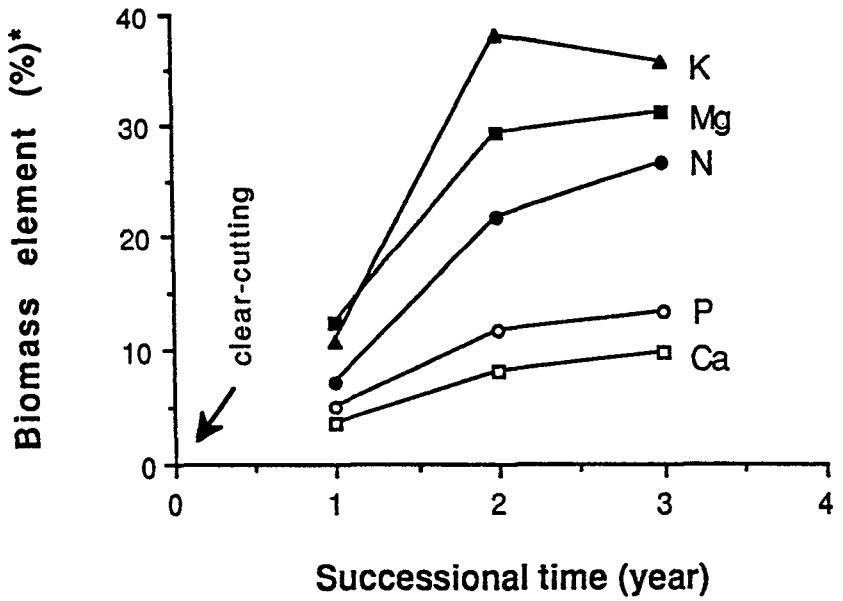

Fig. 5. Accumulation of some nutrient elements in aboveground biomass at Coweeta, North Carolina over three years following clearcutting (Data from Boring et al. 1988). *Amounts of nutrient elements in biomass were transformed into percentage to the corresponding values of uneven-aged forest.

As a matter of fact, decreasing soil P availability is frequently observed with developing time of ecosystems (e.g., Walker et. al. 1981, Black and Marion 1984). These trends would be ascribed to biological immobilization, relatively less rock weathering input and high retention of P in organic materials and inorganic soil minerals.

Several experiments on stream chemistry support the BIH in the case of N (Vitousek 1977, Gimm 1987), but P loss during ecosystem development is not explained by the hypothesis. It should be noted that with ecosystem succession excess P supply may decline due to biochemical mineralization (McGill and Cole 1981). Phosphorus is also increasingly retained by association of soil minerals and humic materials (Kwong and Huang 1978, Elliott 1986). Hobbie and Likens (1973) found that in Hubbard Brook Experimental Forest, annual loss of large particulate P was 12 times higher at a disturbed watershed than at a undisturbed watershed, where total dissolved P export was lowest. Sulfate loss may deviate from the BIH (Table 2) because it is released from organic matter by both biological and biochemical mineralization and adsorbed onto soil particles relatively strongly

and/or because during forest succession maximum organic accumulation rate of S is possibly later than that of N, as discussed with Figure 3.

The sequence presented in Figure 4 is consistent with that of mineralization rates of these soil organic elements as simulated by Parton et al. for grassland soils (1988). Muller and Berg (1988) observed slower release of organic N than that of organic C from decomposing roots of red clover during 196 day-incubation. Conservativeness of organic P is almost universal. Losses of organic C from three grassland soil associations of the Canadian Prairies exceeded those of organic P during long (60 to 70 years) cultivations (Tiessen et al. 1982). Lower mineralization rates of organic P also were observed during decomposition of plant litter (Fenchel and Harrison 1976, Dalal 1979, Staaf and Berg 1982, O' Connell and Menage 1983). Rapid release of C, N, and S from decomposing materials and the suggested sequence can be also substantiated by the comparably low ratios of these elements to P in soil organic matter (Table 1). Sometimes, reported are earlier losses of organic S than N and sometimes even C during leaf litter decay and soil mineralization (Tabatabai and Al-Khafaji 1980, Staaf and Berg 1982, O' Connell and Menage 1983, Mueller-Harvey et al. 1985, Yavitt and Wieder 1988). In effect, completeness of validation requires considering the interactions of organic elements and soil minerals (Anderson 1988). For example, organic compounds of phosphate and sulfate can become stable by sesquioxides (Stewart 1984). Organic elements seem to be protected by clay minerals in the order of P, S, N, and C, but further studies are required (Anderson et al. 1981). More organic N than S was generally mineralized during an eight-week incubation of five Gleysolic soils and their particle-size fractions (Lowe and Hinds 1983). There is also a good illustration that cultivation causes the relatively more losses of organic N than S and that N/S ratios were narrower in the organic matter of cropped soils than in that of virgin soils (see Stevenson 1986, p.303).

Disturbance triggers nitrate fluxes into streams, but may not induce much dissolved P loss due to its microbial and chemical immobilization by soil constituents (Cole et al. 1977, Wood et al. 1984). Again in Hubbard Brook Experimental Forest, the concentration of dissolved P in streams increased little after clearcutting (Hobbie and Likens 1973). McComb (1982, cited by Attiwill and Leeper 1987) provided critical data by comparing total N and P concentrations in

streams and the proportion of land cleared in catchments of the Murrary River basin, Western Australia. Against increase of area cleared in the catchments, total N concentration was increased with apparently steep slope, while that of P was very slightly increased. This only partially supports the hypothesis of Figure 4 because there are no data for S.

VIII. Ecological Implications and Suggestions

It is ecologically important that P become less leaky with ecosystem development, if accumulation of organic C, N and S in ecosystems is largely dependent on P availability (Walker and Adams 1958, Walker and Syers 1976, Stewart 1987). Ecosystems may have a tendency to conserve the more essential elements than the nonessential (Vitousek and Reiners 1975). Similarly, a few key elements will be conserved preferentially once ecosystems have a restricted nutrient retention capacity. Ecosystems would then develop by scavenging some nutrients from the atmosphere on the basis of the conserved elements. In the same context, mineralization of organic P is retarded and even mineralized P is stored inside the soil systems, while much organic N is mineralized and lost to the atmosphere and aquatic systems. During the developing stages of ecosystem, a large fraction of N is supplied from the atmosphere, while most of the P is supplied from internal components.

Preferential P conservation is because terrestrial ecosystem development is based on soil as the element source and there is little alternative P source besides soil component itself. Nutrient retention with ecosystem development is not simply a result of biological adaptation. It may be viewed that increasing P retention with ecosystem development is a result of ecosystem processes or that the constraint of restricted P availability has selected a system which conserves and efficiently uses P. Phosphorus could be a major constraint of biological evolution due to its unique characteristics, such as little atmospheric supply, strong immobility and recycling processes by biochemical decomposition, which all lead to less P availability of autotrophs in the soil environment. Anyhow, subsequent ecosystems might tend to reduce P loss or increase P conservation.

The purpose of this essay was not to put biological processes over abiotic ones, at

least in ecosystem studies. As shown in Figure 1, each process is under the constraint of the other. Just as man has several warehouses, ecosystems can have more than one storage component. Soil is a major constraint for the fate of a terrestrial ecosystem since the biotic component is replaceable, as seen by succession, whereas the soil can be changed but not be substituted. This does not mean that biotic components are less important than abiotic ones. Initial colonization of organisms are largely restricted by soil conditions. Once an area is colonized, interactions of biotic and abiotic processes govern ecosystem development as new organisms modify element distribution in both evolutionary and successional stages through biogeochemical processes (Reiners 1986, Miles 1987).

Fluvial conditions may give only partial information on nutrient retention capacity of terrestrial ecosystems. The BIH should include atmospheric outputs for N and S for reliable test. If loss to the atmosphere is minor or proportional to that of aquatic systems, the latter may be an index indicating nutrient leakiness in terrestrial ecosystems. Furthermore, stream chemistry complicates interpretation on nutrient retentiveness in terrestrial ecosystems because it pools leaf fall input and also is controlled by aquatic processes. In this respect, only nutrient export at the outlet of a watershed would indicate nutrient loss from a watershed itself.

Cation retention has not been discussed in the present study. It may be considered as a counterpart of anion processes, which seem to be controlling factors. More information is required to satisfactorily describe the dynamics of both anions and cations with ecosystem development. For example, comparative studies are expected on other intra- and extra-cellular chemical processes including H ion production during oxidation and reduction of elements (Binkley and Richter 1987, de Vries and Breeuwsma 1987, Miles 1987).

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